Decomposing Phylodiversity

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ABSTRACT

Keywords: Entropy, Biodiversity, Phylogenetic diversity, Functional diversity.

We unify the definitions of phylogenetic and functional entropy and diversity as a generalization of HCDT entropy when an ultrametric tree is considered. We derive the decomposition of phylodiversity and its estimation bias correction to allow its estimation from real, often undersampled data.Phyloentropy can be transformed into phylodiversity to provide a measure of true diversity, i.e. an effective number of species or communities.

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Introduction

Diversity partitioning using conventional species-neutral approach (based on Hill numbers, *i.e.* the effective number of species) is now being replaced by far more interesting frameworks taking into account the species relatedness. This is what we call 'phylodiversity'(Webb, Losos & Agrawal 2006), *i.e.* how species assemblages are distributed in a phylogenic tree. When bothrelative abundance and relatednessdegree between species (or individuals) are quantified, Pielou(1975)suggested that diversity measures should be generalized integrating taxonomic differences between species. A little later, Rao (1982) proposed that the average of the species differences can be used as a measure of biodiversity. Despite some attempts to take into account phylogenic diversity into a generalized species richness (Vane-Wright, Humphries & Williams 1991), this 'avant-garde' ideahas been hardly applied in ecology (e.g. Warwick & Clarke 1995; Crozier 1997).During the last decade, increasing interests into the evolutionary history of communities (Webb 2000) as well as the need for conservation strategies taking phylogenetic risks into account (Faith 2008) revived the interest in phylodiversity partitioning.

Phylogenetic trees are built upon thegenetic similarities and differencesamong various biological individuals or other superior taxa.In a given local assemblage, phylogenetic diversity aims to quantify the evolutionary history shared among individuals since the time of the most recent common ancestor(Chao, Chiu & Jost 2010). All else being equal, an assemblage of phylogenetically divergent species is often seen as more diverse than a local assemblage of closely related species (Vellend *et al.* 2010). There is increasing interest to partition this

phylogenetic diversity not only between local communities but also between time periods in order to elucidate community assembly rules(Pavoine, Love & Bonsall 2009) and investigate what is commonly called the phylogenetic structure of communities (e.g. Cavender-Bares *et al.* 2004). For instance, Hardy & Senterre (2007)argued that a proper partitioning of phylodiversity is a necessary step prior to deciphering phylogenetic clustering (either due to local speciation of allopatric clades or habitat filtering of phylogenetically conserved traits) fromphylogenetic overdispersion (allopatric speciation of two ancestral sympatric species, habitat filtering of phylogenetically convergent traits, competitive exclusion of related species).

Functional trees differ from phylogenetic trees as phylogenetic trees reflect evolutionary constraints while functional trees also take into account ecological convergence (Herault 2007). Each time a proper functional tree can be constructed from a functional trait-based distance matrix (Podani & Schmera 2007), it should be possible to estimate and partition functional diversity in a mannersimilar to phylogenetic diversity(Petchey & Gaston 2002). Functional diversity was often defined as the extent of functional differencesamong individuals or species in a local community (Tilman 2001), animportant determinant of ecosystem processes (Loreau *et al.* 2001). Functional diversity based on functional trees is a great tool to estimate the complementarity among individuals' or species' trait values by estimating their dispersion in trait space at all hierarchical scales simultaneously, avoiding discretization of continuous trait variation into functional groups (Petchey & Gaston 2002). However, functional differences among species or individuals being assessed by a number of *a priori* important functional traits, the degree of similarity among species and, *in fine*, the functional diversity value itself will both depend strongly on this*a priori* choice of functional traits(Weiher *et al.* 1999).

In this paper, we consider that all individuals or species of a local community take place in an ultrametric phylogenetic or functional tree. The distance between two species is measured as the length of the branches between them and their first common node. Chao, Chiu and Jost (2010) generalized Hill numbers to measure phylogenetic or functional diversity (we will often write *phylodiversity* and *phyloentropy* for short) while Pavoine, Love and Bonsall (2009) generalized HCDT entropy(Shimatani 2001; Ricotta 2005 had already done it, but for Rao's quadratic entropy only). We first show here their equivalence: phyloentropy is transformed into phylodiversity the same way HCDT entropy is transformed into diversity *sensustricto*. Then, we derive phylodiversity partitioning as a straightforward generalization of that of HCDT diversity.Finally, we provide estimation-bias corrections for phyloentropy in order to obtain bias-corrected measures of phylodiversity.

Partitioning phylodiversity

Tsallis entropy

Tsallis entropy, also known as HCDT entropy (Havrda & Charvát 1967; Daróczy 1970; Tsallis 1988) has proven to be a powerful tool to measure diversity, generalizing the classical indices of diversity, including the number of species, Shannon and Simpson indices. The order of diversity q gives more or less importance to rare species. Entropy can be converted into diversity *sensustricto*(Hill 1973; Jost 2006), easy to interpret and compare. Estimators of diversity are intrinsically biased because of unseen species and also because they are not linear functions of probabilities (Marcon *et al.* submitted). This is a serious issue (Dauby & Hardy 2012; Beck,

Holloway & Schwanghart 2013), even if some bias corrections are available for HCDT entropy estimators (Grassberger 1988; Chao & Shen 2003; Marcon *et al.* in press).

Neutral diversity

We first recall some features of HCDT diversity partitioning (Marcon *et al.* in press). Consider a metacommunity made of several local communities. Abundances of species in each local community is denoted $n_{s,i}$ ($s = 1, 2, \dots, S$ is the index of species, i the index of communities). n_s is the number of individuals of species s in the metacommunity, n_i the number of individuals sampled in local community i and n the total number. The same notations are used for probabilities of occurrence $p_{s,i}$ which are unknown but estimated with $\hat{p}_{s,i} = n_{s,i}/n_i$. Community weights are w_i: they may be equal to n_i/n but any positive values summing to 1 are allowed. Probabilities in the metacommunity depend on these weights: $p_s = \sum_i w_i p_{s,i}$. Diversity of the metacommunity is γ diversity. Diversity of local communities is α diversity. The formalism of deformed logarithms is appropriated: it allows elegant and intuitive algebra. The logarithm of order q is defined as:

$$\ln_q x = \frac{x^{1-q} - 1}{1 - q} \tag{1}$$

Its inverse function is the deformed exponential:

$$e_q^x = [1 + (1 - q)x]^{\frac{1}{1-q}} \tag{2}$$

Note that:

$$e_q^{x+y} = e_q^x e_q^{\frac{y}{1+(1-q)x}} \tag{3}$$

Tsallis entropy of the metacommunity, $^qH_\gamma$, can be written as:

$$^qH_\gamma = \frac{1 - \sum_s p_s^q}{q - 1} = -\sum_s p_s^q \ln_q p_s \tag{4}$$

Last, diversity is the deformed exponential of entropy, $^qD_\gamma = e_q^{\,^qH_\gamma}$, and entropy is the deformed logarithm of diversity: $^qH_\gamma = \ln_q {}^qD_\gamma$.
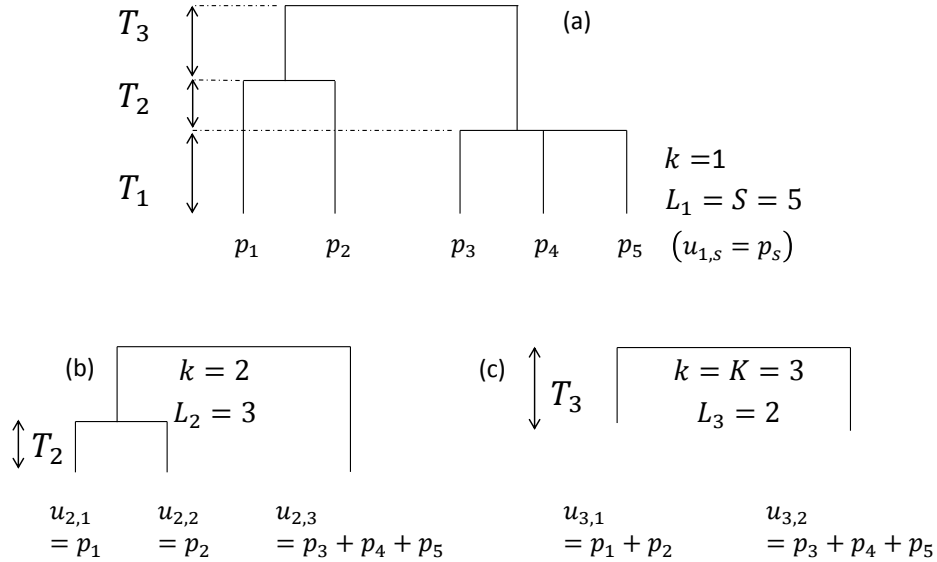
Phyloentropy and Phylodiversity

Figure 1: Hypothetical ultrametric tree. (a) The whole tree contains three slices, delimited by two nodes. The length of slices is T_k. b) Focus on slice 2. The tree without slice 1 is reduced to 3 leaves. Frequencies of collapsed species are $u_{k,l}$. c) Slice 3 only.

Consider a phylogenetic or functional ultrametric tree (**Figure 1**).The first slice starts at the bottom of the tree and ends at the first node. In slice$k$,L_k leaves are found. The probabilities of occurrence of the species belonging to branches that were below leaf l in the original tree are summed to give the grouped probability$u_{k,l}$.

We follow Pavoine, Love and Bonsall (2009) to define phyloentropy as the sum of the entropies in each tree slice, weighted by the slice height. However, we choose to normalize it by the total tree height, $T = \sum_{k=1}^{K} T_k$. We denote it $^q\bar{H}(T)$:

$$^q\bar{H}(T) = \sum_{k=1}^{K} \frac{T_k}{T} \, {}_k^qH$$

(5)

$_k^qH$ is HCDT entropy in slice k. It is calculated as $_k^qH = -\sum_s u_{k,l}^q \ln_q u_{k,l}$.

Chao, Chiu and Jost (2010) generalized Hill numbers to phylogenetic diversity, defined as:

$$^q\bar{D}(T) = \left(\sum_{k=1}^{K} \frac{T_k}{T} \sum_{l=1}^{L_k} u_{k,l}^q \right)^{\frac{1}{1-q}}$$

(6)

Simple algebra shows that:

$$^q\bar{D}(T) = e_q^{\,^q\bar{H}(T)}$$

(7)

This relation is exactly the same as the relation between HCDT entropy and diversity. In other words, phyloentropy is the weighted average of entropy along the tree, and phylodiversity is its Hill number. Entropy is linear, it can be summed over slices, but diversity is not: phylodiversity is not the weighted average of diversity along the tree.

Decomposition

Marcon *et al.* (in press) derived the decomposition of HCDT entropy, generalizing Shannon entropy partitioning (Rao & Nayak 1985; Marcon *et al.* 2012), based on Patil and Taillie's concept of diversity of a mixture (Patil & Taillie 1982). Note that it differs from Jost's

(Jost 2007) non-additive partitioning when community weights are unequal; see Marcon *et al.* (in press) for a full discussion.

$$^qH_\gamma = \ ^qH_\alpha + \ ^qH_\beta = \sum_i w_i \ ^q_iH_\alpha + \sum_i w_i \ ^q_iH_\beta \tag{8}$$

αandβ entropies are the weighted sums of local community entropies $^q_iH_\alpha$ and $^q_iH_\beta$

$$^q_iH_\alpha = -\sum_s p^q_{s,i} \ln_q p_{s,i}$$

$$\tag{9}$$

$$^q_iH_\beta = \sum_s p^q_{s,i} \ln_q \frac{p_{s,i}}{p_s}$$

Since phylogenetic entropy is a linear transformation of generalized entropy, its decomposition is identical and follows equation (8). Inslice$k$, HCDT γentropy is denoted $^q_kH_\gamma$, and the contributions of local community$i$ to α and β entropy are $^q_{k,i}H_\alpha$ and $^q_{k,i}H_\beta$. This can be summed over slices and rearranged to obtain the decomposition of γ phyloentropy:

$$\sum_k \frac{T_k}{T} \ ^qH_\gamma = \sum_k \frac{T_k}{T} \sum_i w_i \ ^q_{k,i}H_\alpha + \sum_k \frac{T_k}{T} \sum_i w_i \ ^q_{k,i}H_\beta$$

$$\Leftrightarrow \ ^q\bar{H}_\gamma(T) = \sum_i w_i \sum_k \frac{T_k}{T} \ ^q_{k,i}H_\alpha + \sum_i w_i \sum_k \frac{T_k}{T} \ ^q_{k,i}H_\beta \tag{10}$$

$$\Leftrightarrow \ ^q\bar{H}_\gamma(T) = \sum_i w_i \ ^q_i\bar{H}_\alpha(T) + \sum_i w_i \ ^q_i\bar{H}_\beta(T) = \ ^q\bar{H}_\alpha(T) + \ ^q\bar{H}_\beta(T)$$

The deformed exponential of equation (8) is the decomposition of phylodiversity:

$$^q_\gamma\bar{D}(T) = \ ^q_\alpha\bar{D}(T) \ ^q_\beta\bar{D}(T) \tag{11}$$

$$\,_\gamma^q\overline{D}(T) = e_q^{\,^q\overline{H}_\gamma(T)}; \,_\alpha^q\overline{D}(T) = e_q^{\,^q\overline{H}_\alpha(T)}; \,_\beta^q\overline{D}(T) = e_q^{\frac{^q\overline{H}_\beta(T)}{1+(1-q)\,^q\overline{H}_\alpha(T)}}$$

α and γ phylodiversities can be interpreted as an equivalent number of neutral species, that is to say the number of species equally different from each other (*i.e.* in an ultrametric tree made of a single slice) with the same probability of occurrence that would give the same measure of diversity. β phylodiversity is an equivalent number of communities, that is to say the number of completely distinct neutral communities with the same weight as actual ones, that would yield the same β diversity as the actual metacommunity.

Bias correction

α and γ HCDT entropies can be corrected following Marcon *et al.* (in press): when q is low, unsampled species are the main issue that can be corrected according to Chao and Shen (2003); when q is high, the contribution of rare species to entropy is small so the bias they cause is little but entropy is less linear with respect to probabilities, requiring the correction of Grassberger (1988). Bias correction relies on the number of sampled individuals (probabilities are not enough) and can be computed for positive values of q. The unbiased estimators are denoted $^q\widetilde{H}$ instead of $^q\widehat{H}$. Their formulas are in Marcon *et al.* (in press) and are not repeated here.

Phyloentropy can be corrected by summing the bias-corrected estimators of HCDT entropy in each slice of the tree. Bias-corrected α entropy, $^q\widetilde{H}_\alpha(T)$, relies on values of $_{k,i}^q\widetilde{H}_\alpha$, the bias-corrected estimators of HCDT α entropy in slice k in local community i.

$$^q\widetilde{H}_\alpha(T) = \sum_i w_i \sum_k \frac{T_k}{T}\,_{k,i}^q\widetilde{H}_\alpha \tag{12}$$

Since the number of individuals in each leaf $u_{k,l}$ increases in slices close to the root of the tree, the bias decreases with k.

${}^q\widetilde{H}_\gamma(T) = \sum_k \frac{T_k}{T} {}^q_{k,i}\widetilde{H}_\gamma$ is calculated the same way. βphyloentropy is obtained as the difference between ${}^q\widetilde{H}_\gamma(T)$ and ${}^q\widetilde{H}_\alpha(T)$ because Grassberger's correction is not available to allow direct calculation.

Example

We used the tropical forest dataset alreadyinvestigated by Marcon *et al*. (2012) and Marcon *et al*. (in press). Two 1-ha plots were fully inventoried in the Paracou field station in French Guiana. 1124 individual trees (diameter at breast height over 10 cm) have been sampled among 229 species. The phylogenetic tree was built introducing a rough taxonomy of the 229 species in the analysis: distance between species of the same genus is set to 1, 2 for different genera of the same family, and 3 for different families. The functional tree was based onspecies relatedness using four key functional traits related to one axis of the leaf-height-seed-stem economic spectra of tropical trees (Baraloto *et al.* 2010b): seed mass and tree maximum height (Herault *et al.* 2011)plusspecific leaf area and wood specific gravity (Baraloto *et al.* 2010a).The functional tree was built from a Gower's similarity matrix agglomerated using Ward's method (full details in Herault & Honnay 2007). Phylogenicdiversity was calculated with the *entropart* package (Marcon & Hérault 2013)under R (R Development Core Team 2014): bias-corrected entropy was calculated first, summed and finally transformed into diversity. Necessary R codes are in Appendix 1.

We first calculated the neutral, phylogenic and functional diversity of order 1 of the metacommunity (the two plots) and partitioned it (each plot is considered as a local community, weights are proportional to the numbers of individuals). The γ neutral diversity (Hill number of Shannon entropy) is 134 effective species, partitioned into α diversity equal to 92 effective species (82 and 107 in each plot) and β diversity equal to 1.46 equivalent communities. Phylogenetic and functional diversity values respectively are: ${}^{1}_{\gamma}\overline{D}(T)$=55 and 5.9, ${}^{q}_{\alpha}\overline{D}(T)$=42 and 5.5 with ${}^{q}_{\beta}\overline{D}(T)$=1.29 and 1.06. Considering the taxonomy of Paracou species, γ phylodiversity is around 2.5 times smaller than neutral diversity. Functional diversity is only 6 equivalent species, showing an extreme redundancy according to the functional tree (FD is estimated equal to 18 for 297 estimated species).
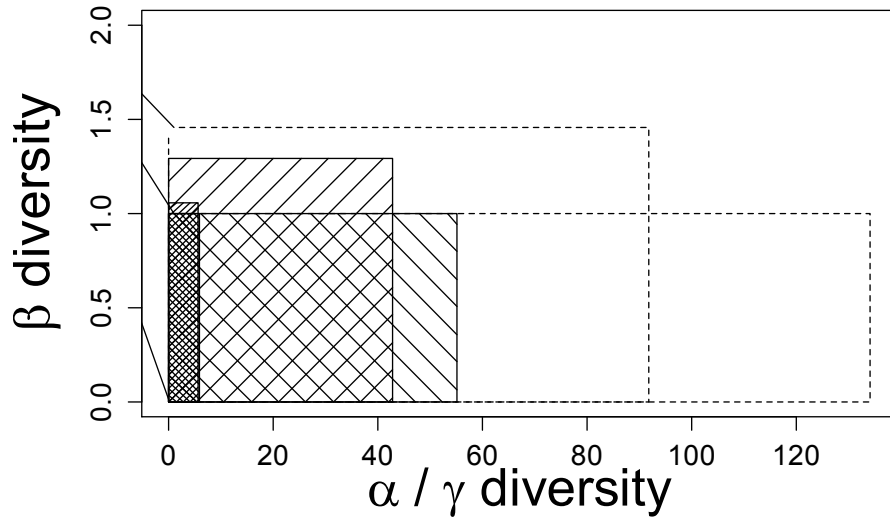

Figure 2: Graphical representation of the diversity of order 1 in Paracou plots. Transparent rectangles represent neutral diversity, hatched rectangles phylogenetic diversity and shaded rectangles functional diversity. In each case, the horizontal rectangle of height 1 represents γ diversity (respectively 134, 55 and 6 effective species). The other rectangle has the same area, but its size is α diversity by β diversity.

Since γ diversity if the product of α by β, they can be represented as nested rectangles (**Figure 2**). The rectangle of size $_\alpha^q\overline{D}(T)$ by $_\beta^q\overline{D}(T)$ has the same area as that of size $_\gamma^q\overline{D}(T)$ by 1. Plotting neutral and phylodiversity together summarizes the essential information: the reduction of diversity due to the consideration of species phylogenetic or functional proximity.
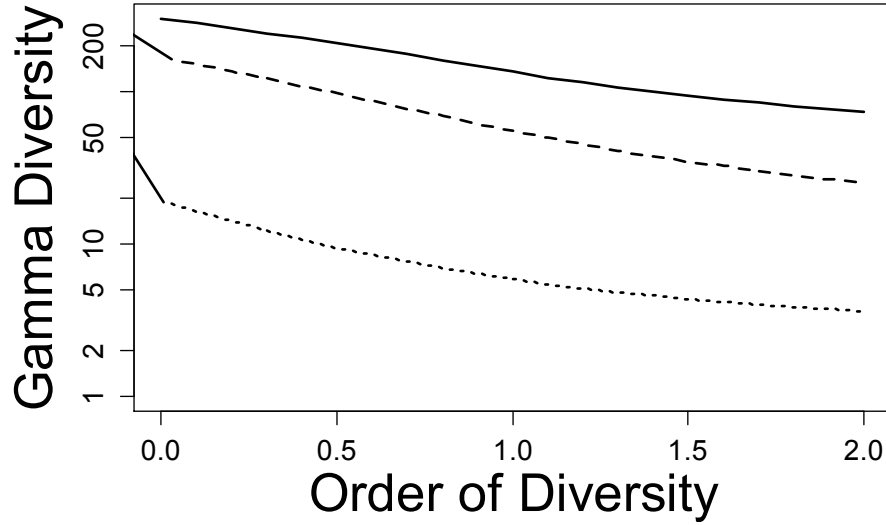

Figure 3: γ Diversity profile of Paracou plots. Neutral diversity (solid line), phylogenetic diversity (dashed line) and functional diversity (dotted line) are plotted against the order of diversity, between 0 (number of species, PD and FD) and 2 (Simpson diversity and Rao's quadratic entropy transformed into diversity), with estimation-bias correction. Diversity scale is logarithmic for readability.

Profiles (**Figure 3**) can be drawn for neutral, phylogenetic and functional diversities.

Discussion and conclusion

Unification of measures of diversity

Phyloentropy generalizes manyprevious indices of diversity. Rao's (1982) quadratic entropy is phyloentropy of order 2 multiplied by T, the tree height. It has been explored in depth and several results obtained here were already known in this special case. It has been partitioned early by Rao himself, weighting communities according to their number of individuals, as Villeger and Mouillot (2008) while Hardy and Senterre (2007) or Pavoine *et al.* (2013) used equal weights. Hardy and Jost (2008) validated both weightings but a general framework allowing additive partitioning of Rao's entropy was missing (Guiasu & Guiasu 2011). We showed that arbitrary weights are acceptable.

Other indices of diversity can be considered as special cases of phyloentropy. We summarize them in **Table 1**.

Table 1: Many usual measures of diversity are special cases of phyloentropy, either reducing it to neutral diversity or limiting it to values of *q* equal to 0, 1 or 2.

	Diversity of order *q*	Special values of *q*
Phylogenetic or functional entropy / diversity	Entropy: $^{q}\bar{H}(T)$ Diverstiy: $^{q}\bar{D}(T)$	$T\left[\,^{0}\bar{H}(T)+1\right]$ equals PD (Faith 1992) and FD (Petchey & Gaston 2002). $T\left[\,^{1}\bar{H}(T)\right]$ equals H_p, the phylogenetic generalization of Shannon's index (Allen, Kon & Bar-Yam 2009).
		$T\left[\,^{2}\bar{H}(T)\right]$ equals Rao's quadratic entropy.
Neutral diversity	Entropy: ^{q}H Diversiy: ^{q}D	$^{0}H+1$ is species richness. ^{1}H is Shannon entropy.
		^{2}H is Simpson entropy.

Conclusion

In this paper, we provide a general, consistent and operational framework to decompose measures of neutral, phylogenetic or even functional diversity into α (within local communities) and β (between local communities) components. We show that entropy can be calculated and its estimation bias corrected in each slice of the phylogenetic or functional tree, summed over slices and finally transformed into diversity. In fact, phylogenetic diversity could be analyzed without using any species concept (*i.e.* without categorizing individuals into a set of species) provided that phylogenetic or functional distance between individuals can be assessed, for example using molecular data or functional trait measured for each member of a meta community (Paine *et al.* 2011). Being able to properly partition phylodiversity is a necessary step towards deciphering the ecological and evolutionary mechanisms that underlie the structure and assembly of communities. Moreover, diversity partitioning will improve our assessment of human-driven modifications of ecosystem functioning in conservation studies.

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Appendix 1: R code of the example

Load the package and the dataset:

```
library(entropart)
data(Paracou618)
```

Calculate diversity

```
# Shannon diversity
DivPart(q = 1, Paracou618.MC, Biased = FALSE)
# Phylodiversity of order 1 based on the taxonomy
DivPart(q = 1, Paracou618.MC, Biased = FALSE, Tree=Paracou618.Taxonomy)
# Functional diversity of order 1
DivPart(q = 1, Paracou618.MC, Biased = FALSE, Tree=Paracou618.Functional)
# FD, with bias correction
DivPart(q = 0, Paracou618.MC, Biased = FALSE, Tree=Paracou618.Functional)
# Number of species
DivPart(q = 0, Paracou618.MC, Biased = FALSE)
```

Plotting Fig.2:

```
data(Paracou618)
q <- 1
# Neutral diversity
(Neutral <- DivPart(q, Paracou618.MC, Biased = FALSE))
par(mar = c(5, 5, 2, 2))
plot(c(0, Neutral$GammaDiversity), c(0, Paracou618.MC$Ncommunities), type =
"n", xlab = expression(paste(alpha, " / ", gamma, " diversity")), ylab =
expression(paste(beta, " diversity")), cex.lab=1.8)
rect(0, 0, Neutral$GammaDiversity, 1, lty=2)
rect(0, 0, Neutral$TotalAlphaDiversity, Neutral$TotalBetaDiversity, lty=2)
# Phylogenetic diversity
(Phylo     <-     DivPart(q,     Paracou618.MC,     Biased     =     FALSE,
Tree=Paracou618.Taxonomy))
rect(0, 0, Phylo$GammaDiversity, 1, angle=135, density=5)
rect(0, 0, Phylo$TotalAlphaDiversity, Phylo$TotalBetaDiversity, density=5)
# Functional diversity
(Functional     <-     DivPart(q,     Paracou618.MC,     Biased     =     FALSE,
Tree=Paracou618.Functional))
rect(0, 0, Functional$GammaDiversity, 1, angle=135, density=20)
rect(0,  0,  Functional$TotalAlphaDiversity,  Functional$TotalBetaDiversity,
density=20)
```

Plotting Fig.3:

```
data(Paracou618)
```

```
Neutral    <-    DivProfile(seq(0,    2,    0.1),    Paracou618.MC,    Biased    =
FALSE)$GammaDiversity
Phylo    <-    DivProfile(seq(0,    2,    0.1),    Paracou618.MC,    Tree    =
Paracou618.Taxonomy, Biased = FALSE)$GammaDiversity
Functional    <-    DivProfile(seq(0,    2,    0.1),    Paracou618.MC,    Tree    =
Paracou618.Functional, Biased = FALSE)$GammaDiversity
par(mar = c(5, 5, 2, 2))
plot(y = Neutral, x = seq(0, 2, 0.1), type = "l", col = "black", lwd = 2,
lty=1, xlab = "Order of Diversity", ylab = "Gamma Diversity", ylim = c(1,
max(Neutral)), log = "y", cex.lab=1.8, main = "")
lines(y = Phylo, x = seq(0, 2, 0.1), lwd = 2, lty=2)
lines(y = Functional, x = seq(0, 2, 0.1), lwd = 2, lty=3)
```